

RESOURCE ASSESSMENT BY ADULT AND LARVAL CODLING MOTHS

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Abstract.—Two-day-old adult and first-instar larval codling moths were assayed for ability to detect and avoid resource sites (=apples) already occupied by conspecifics (i.e., host discrimination). Under laboratory conditions, adults oviposited as readily in the presence of conspecific eggs and larvae as in their absence. Similarly, newly hatched first-instar larvae, when released in laboratory arenas, located and attempted to mount and bore into apples regardless of the presence or absence of older conspecific larvae. We contrast codling moth behavior and ecology with that of two other insect parasites of apple that are known to host-discriminate, the apple maggot fly and the European apple sawfly.

Introduction

Accumulating evidence suggests that individuals utilizing restricted (exhaustible) resources may suffer reduced fitness when living within populations below or above some optimal density range (Peters and Barbosa 1977; Prokopy 1981). Thus, selection may favor individuals that are capable of assessing population density and responding accordingly. Indeed, several different mechanisms have been demonstrated through which foraging animals assess resource quality, quantity, and "population load" of conspecifics, including biochemical, visual, and physical assessment systems (see Prokopy et al. 1982).

For the past several years we have been investigating resource assessment behavior of insects that parasitize (sensu Price 1977) apple fruit. Because individual apples are discrete, exhaustible resource units, we hypothesized that insects that exploit these hosts may avoid apples already occupied by a high density of conspecifics. To date, we have demonstrated that two parasites of apple, the European apple sawfly (*Hoplocampa testudinea*) (Roitberg and Prokopy in MS) and the apple maggot fly (*Rhagoletis pomonella*) (Prokopy 1972) are deterred, by an unknown mechanism and marking pher-

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omone respectively, from ovipositing in developing ovaries and growing fruit respectively, when such hosts are already parasitized by conspecifics. Van Lenteren (1976) defines this "refrainment response" as host discrimination, an ability that has been demonstrated in several entomophagous and phytophagous parasitic insects (Prokopy et al. 1982). In addition to host discrimination by the adults, larvae of *H. testudinea*, when searching for supplemental fruit, avoid hosts occupied by conspecific larvae (Roitberg and Prokopy in MS).

Previous research on resource assessment by a third major parasite of apple, the codling moth, *Cydia pomonella*, is inconclusive. For example, on the basis of distribution of codling moth (CM) eggs and larval-infested apples, Geier (1963) and Jackson (1979) concluded that codling moths probably do not host-discriminate. By contrast, Maclellan (cited in Wood 1965) suggested that freshly laid eggs may deter oviposition by foraging CM females. Van Lenteren et al. (1978) and Mackay and Singer (1982) demonstrated that, when used as the sole criterion, egg distribution data is at best weak circumstantial evidence on which to base conclusions about host discrimination ability.

CM females deposit eggs on or near apples. Following hatch, larvae locate, bore into, and utilize apples for food and shelter. Thus, two very different life forms must make choices of sites for exploitation. Because Ferro and Harwood (1973) demonstrated that individual apples support a finite number of larvae and that competition among larvae may lead to reduced size and fitness of adults, we were particularly interested in determining whether either adults or young larvae could detect presence of and avoid competition with conspecifics.

Materials and Methods

Wild female and male codling moths were collected using an ultraviolet lamp at Orchard Hill, Amherst, Mass. Moths were placed in plastic (11.5 cm × 8.0 cm) cylinders whose walls were covered with waxed paper. Each cylinder was provisioned with one small (ca. 3-cm-diam) apple, serving as an oviposition stimulus (Wearing and Hutchins 1973), and dilute sugar solution. The resulting eggs were held at 24°C, 40–60% R.H., 16L:8D until they matured to the black head stage (just prior to hatch). They then received one of two treatments: (1) transfer to petri dishes for larval behavior assays (see below), or (2) transfer to ca. 10-cm-diam McIntosh apples. In the latter case, resulting infested apples were placed in plastic trays that contained strips of corrugated cardboard which acted as resting and then pupation sites for mature larvae.

Assay of adult discrimination ability.—Following eclosion, female and male moths, reared from the 10-cm-diam apples described above, were

placed in waxed-paper-lined cyclinders at a ratio of 1:2, respectively, to enhance probability of mating and to provide oviposition experience (Roitberg and Prokopy 1981). Females that oviposited while within the cylinders were selected for assays the following day. We performed three different experiments:

Experiment i: Two, 2-day-old females and three male moths were placed in a large ($60 \times 60 \times 25$ cm) Plexiglas-screen cage 5 hr prior to lights off. The floor of the cage was covered with roughened, No. 1 grade filter paper and the front and back walls of the cage were lined with waxed paper to provide an oviposition substrate. The other walls and ceiling remained as screen. Using ScotchTM double sticky tape, we affixed 25 evenly spaced 1-day-old CM eggs, collected as described previously, to one of the waxed-paper walls. To the other waxed-paper wall, we affixed similarly distributed, egg-free double sticky tape. Moths were left in the cages overnight and numbers of freshly-laid eggs were counted the following morning. The orientation of each cage was reversed with each replicate.

Experiment ii: This series of tests was similar to Experiment i except that no eggs were affixed to either waxed-paper wall. Instead, at the base of one waxed-paper wall, we placed two, small (ca. 8-cm-diam) McIntosh apples which were parasitized with two 10-day-old CM larvae. At the base of the other waxed-paper wall, we placed two unparasitized but similar McIntosh apples.

Experiment iii: Electrophysiological tests. We employed whole antennal preparations from 2-day-old CM females. The antennal base was placed on the indifferent electrode and the end of the flagellum on the recording electrode. Output was recorded on a Hewlett Packard FM tape recorder. We presented each of the following substrates 3 cm below each antennal preparation:

- (1) One unparasitized 10-cm-diam apple.
- (2) One 10-cm-old apple parasitized with two 10-day-old CM larvae.
- (3) One glass flask, similar in size and shape to the apples and covered with moist tissue paper (to simulate moisture emanating from apples), to serve as a control.
- (4) One glass microscope slide to which we fastened, with double sticky tape, 25, 16-hr-old CM eggs.
- (5) One glass microscope slide to which we fastened, with double sticky tape, one 10-day-old CM larva (including some of its frass).
- (6) One glass slide to which we fastened double sticky tape, to serve as a control.

Assays of larval discrimination ability.—Experiment i: Individual CM eggs, at the black head stage, were placed in plastic petri dishes (14.5 cm diam) along with and equidistant from (1) one small (8-cm-diam) unparasitized McIntosh apple, and (2) a similar apple parasitized by two 10-day-old CM

Table 1. Response of female codling moths to oviposition substrates with or without conspecifics.

Expt.	Treatment	N	$\bar{X}$ No. eggs laid/♀	P
i	Substrate harboring 25 conspecific eggs	9	10.8 ± 2.1 SE	N.S. X^2
	Substrate harboring no conspecific eggs		10.7 ± 2.4 SE	
ii	Substrate harboring 4 conspecific larvae/2 apples	13	10.3 ± 1.7 SE	N.S. X^2
	Substrate harboring no conspecific larvae/2 apples		11.5 ± 2.5 SE	

larvae. Each dish was oriented in a different direction. In addition, each dish was lined with moist filter paper from which two small circles had been cut. The apples were placed within the circles so that they did not touch the filter paper.

After hatch, larvae crawled on the surface of the filter paper and eventually contacted one of the apples. Due to experimental design, larvae displayed difficulty mounting apples from the filter paper. Therefore, we terminated each replicate when a larva attempted to crawl on an apple, recording search time, and search path of the larva and the parasitization state of the apple. Larvae were disqualified if (1) they failed to initiate search within 90 min, or (2) they crawled out of the petri dish.

Experiment ii: Individual eggs, at the black head stage, were placed on either (1) a small (10-cm-diam) unparasitized McIntosh apple, or (2) a similar apple parasitized by two 10-day-old CM larvae. Larvae were permitted to search on apples until they either (1) attempted to bore into the apple, (2) crawled up the stem, or (3) dropped from it. In the latter two cases, larvae were transferred to apples of the opposite type, and the test was repeated. In both Experiments i and ii, each apple and larva was used only once.

Results

Females oviposited as readily in the presence of conspecific eggs and larvae as in their absence (Table 1). In addition, electrophysiological recordings showed no difference in female antennal response to egg- and larval-treated glass slides compared with control slides. Also, whereas female antennae showed a strong and consistent positive response to whole apples versus none to glass flasks, there were no differences in response to parasitized versus unparasitized apples.

Results from the larval behavior experiments showed that newly hatched larvae do not host-discriminate (Table 2). Similar numbers located and attempted to mount parasitized versus unparasitized apples. In addition,

Table 2. Response of newly hatched codling moth larvae to parasitized and unparasitized apples.

Treatment	Host Condition		P
	Parasitized	Unparasitized	
Expt. ii—Larvae released on host			
Time to arrival at host	$\bar{X} = 8.5 \pm 2.5$ SE (N = 12)	$\bar{X} = 9.2 \pm 2.7$ SE (N = 16)	N.S. Mann-Whitney U
No. turns $\geq 45^\circ$ while searching for the host	$\bar{X} = 8.5 \pm 2.1$ SE (N = 12)	$\bar{X} = 12.2 \pm 3.4$ SE (N = 16)	N.S. Mann-Whitney U
Arrivals at host type	12/28	16/28	N.S. χ^2
Expt. ii—Larvae released on host			
Time until contact with stem base	$\bar{X} = 13.0 \pm 4.6$ SE (N = 14)	$\bar{X} = 9.3 \pm 5.1$ SE (N = 15)	N.S. Mann-Whitney U
Time until boring initiated	$\bar{X} = 15.5 \pm 4.3$ SE (N = 14)	$\bar{X} = 31.6 \pm 9.8$ SE (N = 15)	N.S. Mann-Whitney U
Acceptance of host fruit	14/16	15/16	N.S. χ^2

there were no statistically significant differences in search speed or turning rate of larvae that located either parasitized or unparasitized hosts (Table 2). Similarly, when directly placed on apples, newly hatched larvae readily accepted (i.e., bored into) apples regardless of parasitization state.

Discussion

Resource assessment by most animals is a complex process, shaped in part by ecological, physiological, and phylogenetic constraints. Thus, different animals facing similar foraging problems may, over evolutionary or contemporary time, employ widely different solutions (cf. Wright's "adaptive landscape," Wright 1931). The present study strongly suggests that the codling moth, in contrast to at least two other major parasites of apple (*R. pomonella* and *H. testudinea*), does not partition resources through avoidance of occupied resource sites.

Roitberg (1981) analyzed ecological correlates of phytophagous insects that have been demonstrated to avoid ovipositing at resource sites harboring high density of conspecifics. Correlates common to most of these species included: (1) association with host plants that persist over several parasite generations, (2) comparatively narrow host range, (3) limited mobility of parents and offspring, and (4) restricted sites of parasitization within individual host plants. In addition, Singer and Mandracchia (1982) noted that most, though not all, host-discriminators lay single eggs. While codling moth fits the stereotype of a "typical" host-discriminator, two important differences should be noted. First, adults choose only the proximate area of a host

for subsequent exploitation. It is the larvae that make the final choice as to which apple will be exploited for food and shelter. Second, larvae are relatively mobile and are not restricted to individual hosts. By contrast, *R. pomonella* larvae are unable to emigrate to new hosts should their current host prove unsuitable (pers. obs.).

Our results provide strong evidence that the codling moth does not discriminate against occupied resources. Still, several alternate hypotheses are possible. First, adult host-discrimination behavior may have been adversely affected by experimental conditions, i.e., cage enclosure. We reject this hypothesis on the basis of evidence from moths enclosed in small (ca. 300-cc) containers, where eggs were often distributed in small clusters. In contrast, moths distributed eggs singly in the large assay cages, paralleling the distribution of eggs in nature (Geier 1963). Second, we may have employed such high concentrations of conspecific eggs or larvae that the host assessment system was overstimulated, leading moths to oviposit at random. We are unable to refute or substantiate this hypothesis for codling moth or any other phytophagous host-discriminator. Third, with regard to CM larvae, the physical structure of the arena may have disrupted normal host assessment behavior. Our observation of larval behavior argues against this hypothesis, in that assay larvae moved freely within the assay arenas and appeared to readily detect the presence of both apples present.

Two features of codling moth behavior, while lacking any overt host-discrimination, may provide for reduced competition of offspring. First, adults tend to oviposit in areas of high fruit density (Jackson 1979), thereby providing greater levels of resource availability. Second, each oviposition is preceded and followed by a period of flight (Geier 1963). This action reduces the chance of sib-sib larval competition. Similar behavior has been demonstrated for other insects, including *H. testudinea* (Roitberg and Prokopy 1980) and *R. pomonella* (Roitberg et al. 1982).

Finally, we reemphasize the potential danger of unidimensional, deterministic approaches to studies of insect resource assessment behavior and expectation of universal host-discrimination ability (cf. Gould and Lewontin 1979). Codling moth adult oviposition and larval host-location behavior is probably influenced by several factors, all of which may determine future fitness of individuals. These could include: energetic costs to foraging by adults and larvae, foraging-associated risks to predation, structure of resource patches and abiotic factors. As an example, newly hatched larvae may risk threat to life if resources are not quickly located (Jackson and Harwood 1980). Therefore, host discrimination may be of lesser importance to these animals compared to a species such as *R. pomonella*. The cost of developing and maintaining a host-discrimination information processing system may outweigh the benefits (Jackson 1979). In conclusion, while we may analyze animal behavior from particular theoretical perspectives, we should main-

tain our awareness of the complexity and stochastic nature of behavioral and ecological events.

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